

Abstract.—Seasonal variability in gonad growth was investigated for the tropical cephalopods *Loligo chinensis* and *Idiosepius pygmaeus*. Statolith ageing techniques enabled a comparison of gonad growth in relation to both individual size and age. Age analyses revealed that male and female individuals of *L. chinensis* matured earlier during the warmer summer period than in the cooler winter period. These preliminary results suggested that maturity was governed more by individual size rather than age. Analysis of seasonal change in the gonadosomatic index (GSI) revealed that *L. chinensis* gonad tissue accounted for the greatest percentage of body weight in the month of October. The trend in the nidamental gland/mantle length index closely paralleled the trend in GSI values for female individuals of *L. chinensis*, while growth of the nidamental gland and hectocotylus closely paralleled growth of the gonad. The seasonal variation in reproductive investment for *Idiosepius pygmaeus* followed a different pattern compared with *L. chinensis*. Slower growing cool-season (spring) individuals lived longer and had comparatively larger gonads than their warm-season (autumn) counterparts, despite no difference in body size between the two seasons. *Idiosepius pygmaeus* thus appeared to be employing a 'trade-off' in its reproductive strategy by partitioning a greater amount of energy into gonad tissue over a longer lifespan during the cooler period of the year.

Seasonal variation in reproductive investment in the tropical loliginid squid *Loligo chinensis* and the small tropical sepioid *Idiosepius pygmaeus*

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In reviewing cephalopod reproduction, Mangold (1987) has emphasised that there are at least as many open questions as there are established facts, and that there are thus many gaps in our knowledge as well as contradictory statements. Recent research (e.g., Hanlon et al. 1989, Rodhouse & Hatfield 1990, Jackson & Choat 1992) is revealing that cephalopod lifespans are considerably shorter than many estimates made over the last several decades. This past confusion has apparently led to a poor understanding of the reproductive tactics of cephalopods. Clearly, any ideas regarding the lifespan of an organism will influence ideas regarding reproductive events in the individual.

Statolith ageing techniques have the potential for resolving some of the discrepancies in our understanding of the reproductive tactics of squids and sepioids. By analyzing individual age and maturity status, age-at-maturity and time-specific schedules of gonad growth can be constructed. The focus of this study was to consider seasonal variation in age-at-maturity and reproductive investment in the tropical loliginid squid *Loligo chinensis* and the small sepioid *Idiosepius pygmaeus*. Statolith ageing techniques have been applied to both *I. pygmaeus* (Jackson 1989) and *L. chinensis* (Jackson 1990a, Jackson

& Choat 1992). Analysis of seasonal samples for both of these species has revealed that there was considerable seasonal variation in growth (Jackson & Choat 1992). This study was therefore undertaken to see if there was any seasonal variation in gonad growth or seasonally-induced variation in age-at-maturity in these two species.

Loligo chinensis is common in North Queensland waters and can be captured by bottom trawls throughout all months of the year. The species is sexually dimorphic, with males growing longer than females. In North Queensland waters, males are commonly encountered up to ~180 mm dorsal mantle length (DML), while females are common up to ~120 mm DML. Hatchling size for *L. chinensis* is ~1.4 mm (unpubl. data). In the summer, *L. chinensis* reaches adult size in ~100 d, while winter growth is slower with adult size reached by 140–170 d (Jackson & Choat 1992).

Idiosepius pygmaeus is a common neritic cephalopod which is found in surface waters in mangrove, estuarine, and breakwater habitats (Jackson 1989). This species, however, is only common in nearshore surface waters between March and November, with few specimens observed over the summer months (December–February) (Jackson 1992). *Idiosepius*

pygmaeus is sexually dimorphic, with females reaching much larger sizes than males. In North Queensland waters, males are commonly encountered up to ~10 mmDML, while females are commonly encountered between 13 and 18 mmDML. Planktonic hatchlings are ~1 mmDML (pers. observ.). This species has a short lifespan, with maturity reached in <80 d (Jackson 1989), and exhibits slower growth during the cooler seasons of the year (Jackson & Choat 1992).

Materials and methods

Loligo chinensis and *I. pygmaeus* were captured from tropical waters off Townsville, North Queensland. Preparation and enumeration of statolith growth increments for both species were similar to techniques used for *Sepioteuthis lessoniana* (Jackson 1990b), although statoliths of *I. pygmaeus* were not ground or polished. Individuals of *L. chinensis* were captured in paired trawl nets (each net had an 11 m gape and 3.8 cm mesh) which were towed for ~20 min. The majority of individuals of *L. chinensis* were captured in Cleveland Bay (19°11'S, 146°56'E) in water depth <20 m. Trawling was undertaken generally for one day each month from February 1988 to November 1989, and up to 15 trawls were taken on each sampling date. Individuals of *I. pygmaeus* were captured by dip-netting along a breakwater east of the Townsville harbor (19°15'S, 146°50'E; see Jackson 1992). Individuals of *L. chinensis* used in the age analysis were captured on 12 January 1989 (summer, $n=37$) and 13 July 1989 (winter, $n=27$). Individuals of *I. pygmaeus* were analyzed from autumn and spring. Individuals ($n=41$) for the autumn sample were captured during four sampling periods over two years: 22 and 23 March 1988; 21 and 22 March 1989. Individuals ($n=38$) for the spring sample were from six sampling trips over two months: 10, 23, 24 August 1988; 7, 20, 21 September 1988. The greatest differences in growth rates and population age structure were observed between these two seasonal periods (Jackson & Choat 1992).

Analysis of reproductive structures

Specimens of *L. chinensis* were initially fixed in buffered 10% seawater-formalin to preserve the large tissue mass and later transferred to 70% alcohol to prevent damage to the statoliths. Specimens of *I. pygmaeus* were preserved immediately in 70% alcohol due to their small body size. Gonads were removed, blotted with paper toweling (*L. chinensis*) or filter paper (*I. pygmaeus*), and weighed. Dorsal mantle length (DML) was measured on both species, and nidamental gland length

(NGL) and hectocotylus length was measured on female and male individuals of *L. chinensis*, respectively. Measurements were taken with an eyepiece micrometer (*I. pygmaeus*) or with either callipers or a graduated ruler (*L. chinensis*). Maturity was determined by the presence of mature oocytes in the ovary along with large nidamental glands in females, and the presence of spermatophores in males.

To discern the pattern of growth for gonads, the nidamental gland, and the hectocotylus, measurements of gonad weight, nidamental gland length, and hectocotylus length were plotted against both mantle length and age. Due to the large amount of scatter in many of the plots (especially with *I. pygmaeus*) and the complex curvilinear relationship between many of the relationships, regression analyses were not carried out.

Gonadosomatic and NDL/DML indices

The seasonal trend in gonad growth was also examined for *L. chinensis*. Maturity status was determined for 231 individuals from trawl samples between February 1988 and November 1989 (this analysis included data from individuals which were aged from the January 1989 and July 1989 samples). For most samples, all individuals within the adult size-range (>100 mm) were used in the gonad analysis, except for several summer samples in which a very large number of individuals >300 mm were captured.

Parameters measured for each squid were dorsal mantle length, body weight, gonad weight, and nidamental gland length for females. The gonadosomatic index (GSI) was calculated for each specimen as

$$\frac{\text{gonad weight (g)}}{\text{total body weight (g)}} \times 100.$$

For females, the nidamental gland length/dorsal mantle length (NGL/DML) index was also calculated as

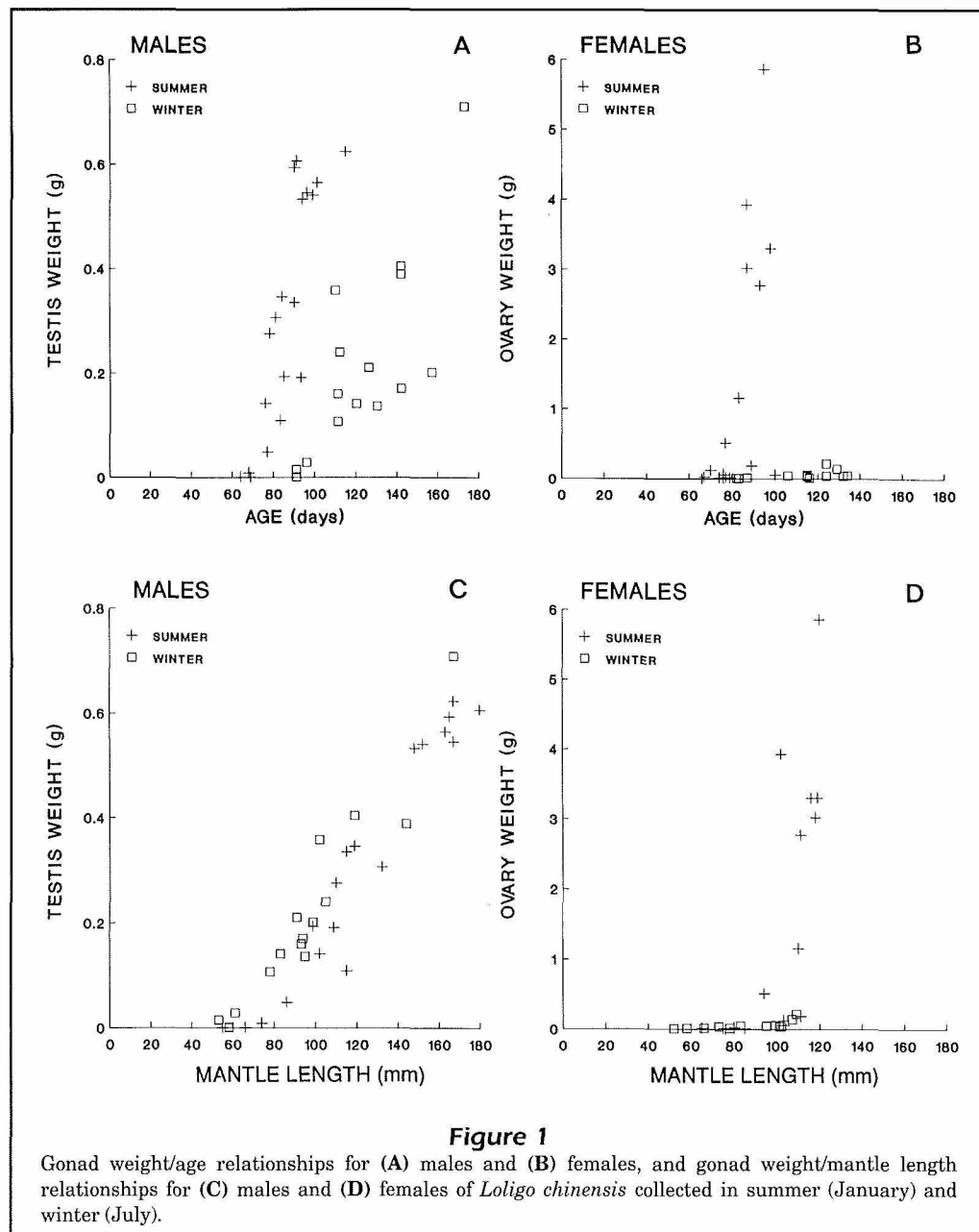
$$\frac{\text{nidamental gland length (mm)}}{\text{mantle length (mm)}} \times 100.$$

Analyses of nidamental gland length and hectocotylus length were not carried out for *I. pygmaeus*.

Results

Loligo chinensis

Gonad growth with age There were differences in the relationship between gonad weight and age for the two samples of *L. chinensis* taken within different seasonal periods (Fig. 1A,B). The relationship between testis weight and age was similar during both sea-



sons, with the main difference being the shift in the winter curve to the right (Fig. 1A). Because of seasonally-induced differences in somatic growth (Jackson & Choat 1992), males matured later in winter. The relationship between age and testis weight had greater variability in winter, which suggests that age-at-maturity was less well-defined in the winter, with a slower rate of maturity in some individuals.

In both winter and summer, males with a testis weight >0.1 g had spermatophores present. However, there was variability in age-at-maturity in both seasons, with testis weight in apparent immature males of 0.307–0.335 g. The youngest mature male during

summer and winter was 83 d and 111 d, respectively. The oldest immature males for summer and winter were 90 d and 130 d, respectively.

There were also seasonal differences in maturity patterns of females based on ovary weight (Fig. 1B). Females matured in summer at a young age, with the ovary reaching a large size in 65–85 d, although two older specimens were immature. This was especially apparent in the oldest individual (100 d) which also had very undeveloped nidamental glands.

All females in the winter sample had small gonads and nidamental glands, and there were no mature or soon-to-be-mature females. This differed from the pat-

tern observed in males, which had reached maturity in winter, and suggested that female maturity was out of phase with males during this period of the year.

All females aged in summer with an ovary weight >1.161 g were mature, and the ovary filled much of the mantle cavity. The youngest mature female was 83 d, while the oldest immature female was the oldest female aged, 100 d.

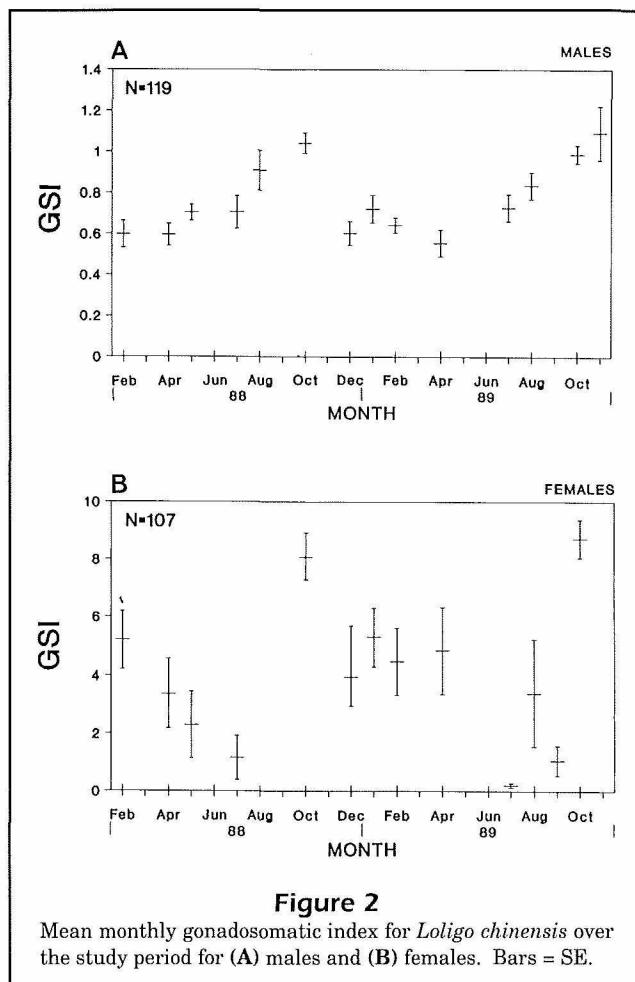
Gonad-soma relationships Comparing gonad weight to individual age (Fig. 1A,B) revealed a different pattern than in the gonad weight/mantle length analysis (Fig. 1C,D). Despite the fact that there was a noticeable difference in the testis weight/age scatter plot (Fig. 1A), due to the older winter males, the testis weight/mantle length relationship was similar for both seasons (Fig. 1C). Thus gonad increase was proportional to the squid length rather than its age.

A different pattern emerged when comparing ovary weight/mantle length relationships for female *L. chinensis* (Fig. 1D). Although the lack of maturity was still obvious in winter females, the gonad weight/mantle length relationship for both seasons resulted in a single curvilinear relationship, suggesting that maturity occurred at 100–120 mmDML, regardless of age. Furthermore, although this ageing study indicated that a large proportion of the winter females were older than their summer counterparts, many of the winter immature females were smaller than squids captured in the summer. As with the males, squid size rather than age may be a better indicator of maturity.

Reproductive indices Although it was possible to determine the ages of only a small number of individuals in two seasons ($n=64$), changes in the gonad weight/soma weight relationship throughout the year were examined. For both males and females, a seasonal trend could be detected in the GSI (Fig. 2). In males, GSI values were low, with $<1.2\%$ of the total body weight consisting of gonad. In contrast, female GSI values were more variable and generally higher than in males, with the gonad comprising as much as 8% of total body weight.

Mature males were found in all months sampled. However, a regular seasonal oscillation in relative gonad weight was apparent (Fig. 2A). There was an increase in relative gonad weight from April to October in both years. Over the two years, the testis accounted for its greatest percentage ($>1\%$) of body weight in October, while its lowest values were recorded in April.

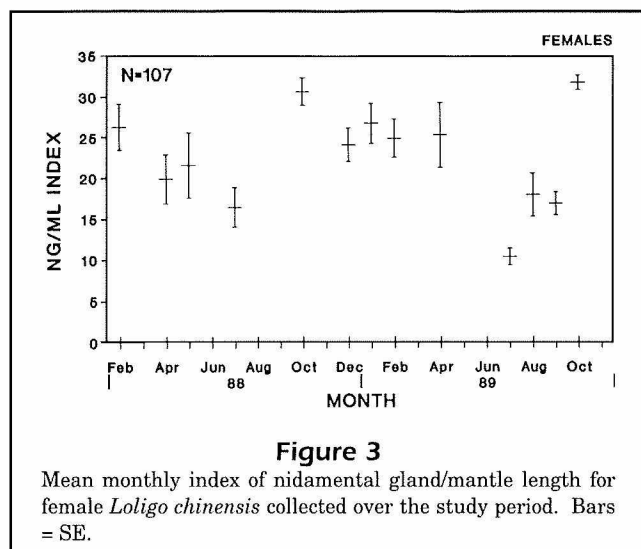
A similar pattern of fluctuation also existed with the female GSI values (Fig. 2B). In October, females consistently had GSI values that were considerably higher than for other months. Mature females were present in all months except July 1989. As discussed



previously, females aged from the 1989 summer sample showed a considerable range in gonad size and level of maturity, despite similarities in both size and age. This range in gonad size was also reflected in the female GSI values, in that the mean values had large standard errors (Fig. 2B) in nearly every month. This was due to the fact that for many months, a proportion of the individuals was immature.

The seasonal trend in the NGL/ML index (Fig. 3) was similar to the trend in the female GSI (Fig. 2B). This index also indicated a greater investment in reproduction during October, with lowest values in July. Furthermore, standard errors were generally less for this index than for the GSI.

The monthly mean mantle lengths for males and females were plotted for the 2 yr period (Fig. 4A,B). Although there was some variation in mantle lengths for the different samples, these could not be related to the seasonal peaks or troughs in the GSI values. For example, the largest females were captured from February to July 1988 (Fig. 4B). However, GSI values dropped considerably over this period. Furthermore, mean mantle length was not highest in October for



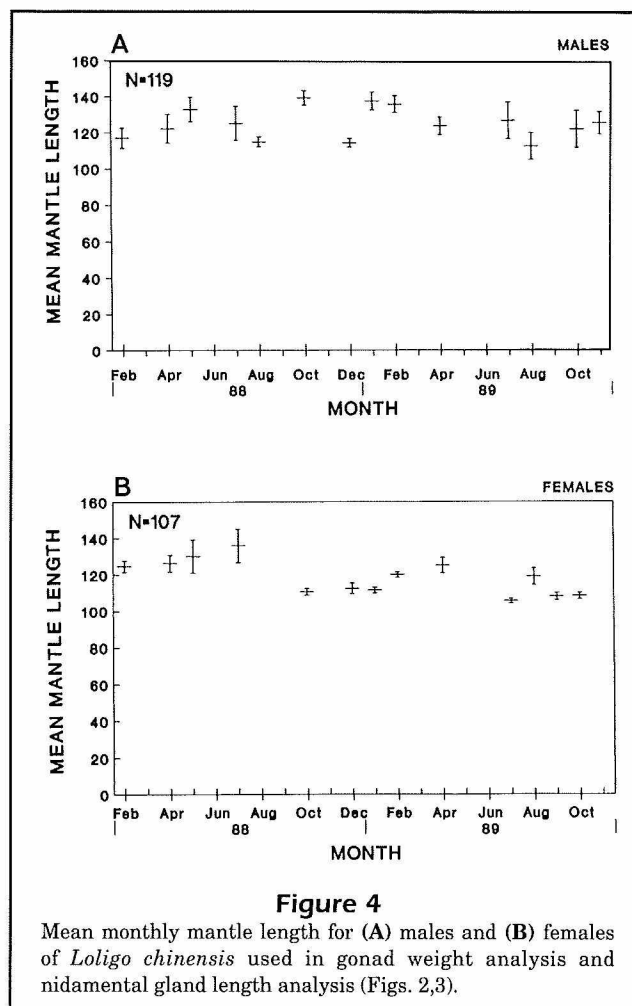
each year, and although 1989 July values were slightly lower than the other months, the July 1988 values were not. The observed changes in relative gonad weight can thus be considered unbiased by individual size.

Nidamental gland and hectocotylus lengths Nidamental gland length was perhaps the most useful measurement in female squids for obtaining an index of maturity. The relationship of nidamental gland length to mantle length and age of female specimens of *L. chinensis* (Fig. 5) closely resembled the ovary weight/age and mantle length relationships for this species (Fig. 1B,D). For example, two separate relationships were apparent when nidamental gland length was plotted against age, whereas both seasons' data points produced one curvilinear relationship for nidamental gland length vs. mantle length. As with the ovary data, these data suggest that nidamental gland length was more closely related to mantle length than to age.

Similarly for males, hectocotylus length vs. mantle length and age (Fig. 6) exhibited the same pattern observed in the testis weight/age and mantle length relationships (Fig. 1A,C). For example, in winter there was a shift along the age axis, producing a separate correlation for the summer hectocotylus length/age data. However, there was some indication that at large sizes, faster-growing (summer) males had a shorter hectocotylus than slower-growing (winter) males. This relationship was similar to the testis weight/mantle length relationships for *I. pygmaeus* (Fig. 7C,D) seen below.

Idiosepius pygmaeus

Gonad growth with age In contrast to *L. chinensis*, within-season variability in maturity and age-specific



trends for *I. pygmaeus* could be determined with a greater degree of accuracy. This was possible because of the greater number of replicate sub-samples taken during each seasonal period (see Methods).

The seasonal pattern of gonad growth was different for *I. pygmaeus* than for *L. chinensis*. The seasonal influence on gonad growth and maturation may have been somewhat less for individuals of *I. pygmaeus* (analyzed for spring and autumn) compared with individuals of *L. chinensis* (analyzed for summer and winter). However, individuals captured in autumn would have grown over the warmer period at the end of summer, while individuals from the spring sample would have grown and matured through the colder period, at the end of winter.

Due to the considerable scatter in age/length relationships for this species (Jackson & Choat 1992), there was also considerable scatter in the gonad weight/age relationship (Fig. 7A,B). While gonad weight/age relationships for *L. chinensis* resulted in different scatter plots separated on the age continuum (x axis), the pattern was modified differently for *I. pygmaeus* for

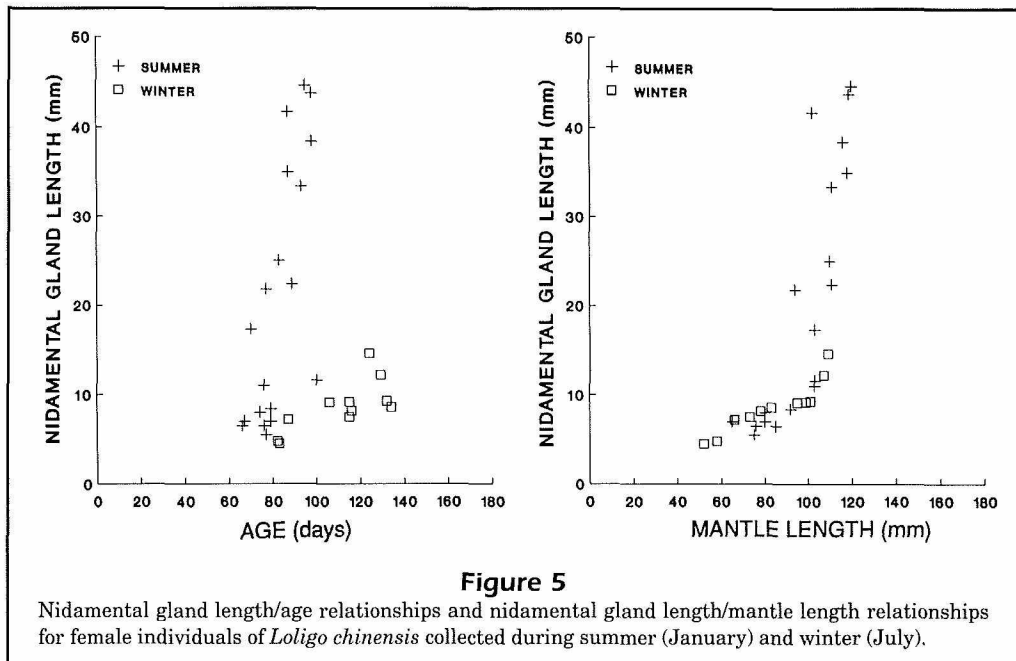


Figure 5

Nidamental gland length/age relationships and nidamental gland length/mantle length relationships for female individuals of *Loligo chinensis* collected during summer (January) and winter (July).

the two seasons (i.e., both seasons' data points fell within the same scatter plot). While individuals of *I. pygmaeus* were older in the spring samples, their gonads reached a proportionally greater weight than did the autumn individuals.

Males The relationship for testis weight vs. age (Fig. 7A) was the same for both seasons, with data points clustering on a single testis weight/age continuum, with the exception of one 41 d individual which

fell considerably outside the cluster of data points. The major difference in the seasonal component of the data was a clustering of data points for each season at opposite ends of the testis weight/age continuum, with spring individuals reaching a greater age and possessing proportionally heavier testes than their autumn counterparts.

The youngest mature males in spring and autumn were 22 d and 37 d, respectively, while the oldest im-

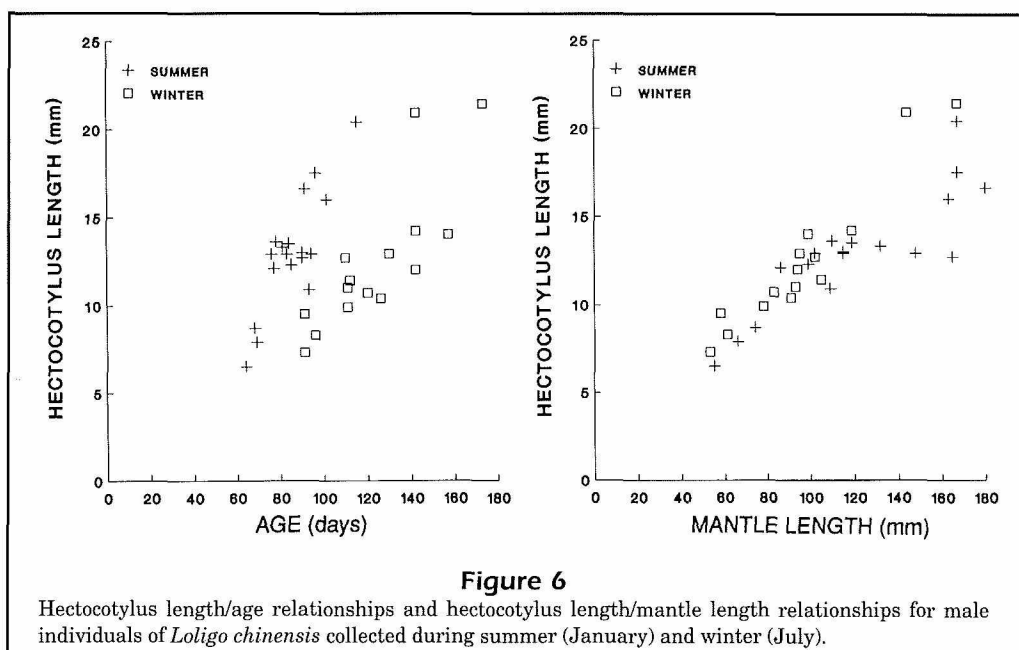
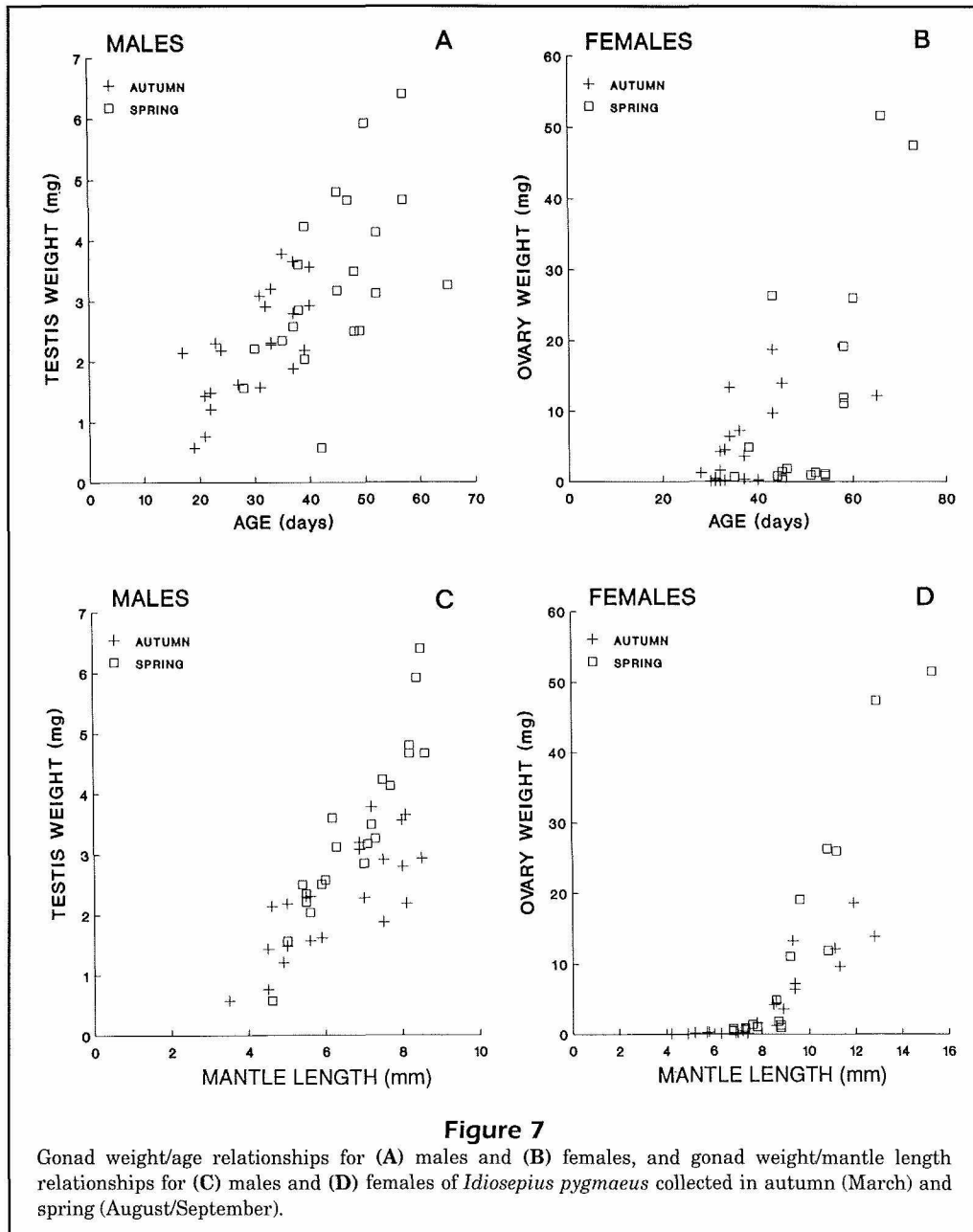


Figure 6

Hectocotylus length/age relationships and hectocotylus length/mantle length relationships for male individuals of *Loligo chinensis* collected during summer (January) and winter (July).



mature males for both seasons were 32 d and 38 d, respectively.

Females A similar relationship to the males also existed in the ovary weight/age relationship, i.e., both seasons' data points tended to cluster along one ovary weight/age continuum (Fig. 7B). However, the scatter was greater than for males, due to the fact that in both seasons there were individuals with very small ovaries. For example, in both seasons, individuals of 40–60 d showed a considerable range in ovary weight. However, as with male testis weight, the spring females also had the heaviest ovaries. Although a num-

ber of females had large well-developed ovaries, none of the specimens examined had any mature ova present.

Gonad-soma relationships One possibility for the greater gonad weight in spring vs. autumn could have been due to larger individuals being captured in the spring. However, the plot of gonad weight against mantle length for both sexes (Fig. 7C,D) revealed no size difference in males between seasons and only one spring female slightly larger than the other females. Although there is some overlap in the data for the smaller individuals for both seasons, in the larger sizes,

slower-growing spring individuals did, in fact, eventually produce larger gonads than their autumn counterparts.

Discussion

The biotic and abiotic influences on maturity are complex. Factors such as light (day length), temperature, and food availability can all affect rate and age-at-maturity. Gonad development is directly under hormonal control, and appears to be influenced by the optic gland (Mangold 1987, Boyle 1990). However, the process of maturity is not completely understood and may also be controlled to a certain degree by individual genetic factors, apart from outside influences (Mangold 1983). This study gives preliminary insight into the maturation process in tropical squids and sepioids based on age information. Statolith ageing techniques should prove useful in providing a time-scale on the squid maturation process and problems encountered with variation in size-at-maturity.

Loligo chinensis

Variability in size-at-maturity appears to be a common phenomenon with cephalopods. Hixon (1980) found that some immature *Lolliguncula brevis* females were as large as other fully-mature individuals. Considerable variation in maturity has also been shown to exist in *L. opalescens*, with females maturing by 81 mmDML while other females remain immature until 140 mmDML (Hixon 1983). Similar discrepancies in size-at-maturity have also been documented for *Sepia officinalis* (Boletzky 1983) and *Dosidicus gigas* (Nesis 1983). Mangold (1983) has also demonstrated that cultured octopuses reared from the same egg mass reached maturity independent of sibling size or age. The delay in maturity for some *L. chinensis* females for a given length (e.g., Fig. 1B, summer) is similar to observations made for *Lolliguncula brevis* by Hixon (1980). However, in contrast to the other studies cited above, *L. chinensis* females do not show a wide difference in size-at-maturity. The fact that maturity was more closely related to length than to age suggests that there might be some physical or physiological mechanisms controlling maturation apart from age. Some female cephalopods have been shown to develop eggs only when a minimum threshold in body size is achieved (Mangold 1987). The maximum size for individuals of *L. chinensis* obtained in this study is smaller than the maximum size recorded for the species, which is up to 300 mmDML (Roper et al. 1984). This suggests that the squids in Cleveland Bay may be a precocious population which is maturing near the mini-

mum threshold in body size for the species. This could therefore account for the restricted size-range at maturity.

Although male and female *L. chinensis* were mature in the same age-range in summer, a different situation existed in winter, suggesting that maturity in the female winter population was out of phase with the males. This situation has been noted with *Todarodes pacificus* in which males reach maturity 3–6 mo earlier than females (Okutani 1983). This may not be an ecological constraint, considering the reproductive tactics of cephalopods. In many species of cephalopods, males mate with immature females (Mangold 1987) with the females retaining the spermatophores until they spawn. An extended interval between mating and spawning has also been noted in octopods, with up to a 114 d interval between spermatophore transfer and spawning (Boyle 1990).

Alternatively, the apparent absence of mature females in July may have been due to inadequate sampling, since the oldest-aged female captured in winter was 134 d whereas males as old as 173 d were captured. Since maturation was rapid (e.g., females matured in <80 d in summer), it is possible that older mature females existed in winter but that none were captured.

Based on previous work on the effect of temperature on growth rate (e.g., Forsythe & Hanlon 1988 and 1989), seasonal differences in water temperature may also account for the lack of gonad development in *L. chinensis* during winter. As age of field specimens in relation to maturity processes has not previously been considered, only aquarium culture experiments are available for comparison. Richard (1966, cited in Mangold 1987) has shown that males and females of the cuttlefish *Sepia officinalis* from the English Channel, which were raised at 20°C, attained sexual maturity at 7 mo and 140 mmDML, while conspecifics raised at 10°C were totally immature at the same age and were only 50 mm in length. Moreover, Richard (1970, cited in Mangold 1987) also found that females of *S. officinalis* raised at 18°C had a gonad index of 8% at 270 d, while it took 480 d for females raised at 13°C to reach the same value. Other factors, such as seasonal variability in food supply and day length may also influence seasonal differences in maturation rates.

The fluctuations of the GSI and NGL/ML index indicated that ambient environmental conditions (e.g., temperature and food availability) were influencing both the maturity process and the energy *L. chinensis* partitioned into reproduction. Although individuals were often mature (e.g., the majority of males analyzed) there were time-periods when the ovary and testes accounted for a greater percentage of total body weight. This was consistently recorded for both sexes

in the month of October, and would coincide with the spring warming of water in Cleveland Bay after low winter temperatures which begin to rise in August/September (Kenny 1974, Walker 1981). Highest GSI values were also reported for male and female *L. vulgaris* during the spring period in the Mediterranean (Worms 1983).

The interpretation of fluctuations in the GSI and NGL/DML index is complex due to a variety of factors: (1) *L. chinensis* exhibits fast growth and has a short lifespan, therefore annual data sets reflect a number of different generations of squids; (2) because of rapid growth and the observed variability in gonad growth (especially in females), greater sample numbers would be needed to adequately describe gonad growth fluctuations on a smaller scale (e.g., intra-monthly variability); (3) due to the tropical nature of the environment, squids (especially males) are mature throughout most months of the year and, therefore, gonad indices are generally reflecting periods of greater investment in reproductive structures rather than periods of immaturity vs. maturity.

The data peaks in October may have been due to the increasing day length in spring, stimulating the optic gland to produce increased hormonal levels which accelerates gonad growth (see Mangold 1987). Since day length would be shortened over the winter period (June–August), the increasing day length during the spring period, along with increasing water temperatures, may produce physiological responses leading to maximal gonad growth. More intensive sampling (e.g., fortnightly) over the late-spring and early-summer period may provide a clearer picture of relative gonad growth over this period. The relationship between mantle length and NGL could constitute a good maturity index for females, since the relationship between NGL and DML is closer than the relationship between DML and gonad weight (Worms 1983). Data for females of *L. chinensis* from this study suggest that the NGL/DML index provides results very similar to GSI values. Maturity parameters based on NGL alone could constitute a more convenient means to determine maturity for tropical squids.

Nidamental gland length The fact that length of the nidamental gland of *L. chinensis* bears a very close resemblance to growth of the gonad highlights the close association this organ has with maturation and egg development. The nidamental gland serves the function of producing a gelatinous matrix which encases the cephalopod egg (Roper et al. 1984). Previous studies have used the NGL/DML ratio as a convenient means to assess maturity. Temperate loliginids have been shown to possess mature oocytes when this ratio is >0.2 (Yang et al. 1986, Hanlon et al. 1989). This

relationship generally holds well for females of *L. chinensis*. Out of 112 females (captured throughout the 2 yr sampling period) analyzed for this ratio, all the mature females had an NGL/DML ratio >0.2 . Of the immature females analyzed, six individuals (5.4%) had a ratio >0.2 (highest value=0.26). This parameter therefore appears to be useful for tropical loliginids as well. The 0.2 NGL/DML ratio does appear to be the minimum parameter for mature females.

Nidamental gland measurements are thus useful for providing a rapid and convenient means of assessing the level of maturity in tropical loliginids. The nidamental gland can also provide useful information about the past history of a female squid. The fact that some of the larger, older, immature females captured during January had small underdeveloped nidamental glands was one means to ascertain that these females had actually not yet matured and had not regressed from a previously mature condition.

Hectocotylus length The hectocotylus is an important reproductive structure employed by the male to pass spermatophores to the female during copulation. It is also extremely useful for quick sexual identification of preserved specimens. Coelho et al. (1985) carried out a detailed study of the growth of the hectocotylus of *Illex illecebrosus* to determine if the degree of hectocotylyzation of the fourth arm could be related to maturity. However, no close relationship was found between maturity and the degree of hectocotylyzation. A partial explanation for this lack of relationship between these parameters was attributed to the fact that the squids examined might have included individuals which hatched at different localities and which had developed under different temperature regimes (e.g., some squids could have been immigrants from a more southerly population exposed to warmer temperatures). This could well account for considerable confusion in the *Illex* data, as individuals of *L. chinensis* from different seasons showed a different relationship between hectocotylus length and mantle length, and hectocotylus length and age. These seasonal growth patterns which were temperature-related did have an influence on the development rate of the hectocotylus, with slower-growing individuals eventually possessing a larger hectocotylus than their faster-growing counterparts. Different-sized hectocotili on similar-sized squids could therefore indicate that the squids had developed under different growth rates. This also suggests that the size ratio of many other structures to body size may also be influenced by the ambient temperature in which the squid develops. Parameter ratios and indices used for taxonomic purposes should therefore be cautiously employed, at least for nearshore squids, and, whenever possible, parameters should be measured in

individuals captured under similar environmental conditions.

Idiosepius pygmaeus

The pattern of gonad maturation in tropical squids and sepoids becomes more complex when the pattern of seasonal maturation of *I. pygmaeus* is also considered. As with *L. chinensis*, individuals of *I. pygmaeus* which grew during a cooler time of the year also reached a greater age. However, gonad maturation was modified in a different way compared with *L. chinensis*. For example, in both seasons males (including mature individuals) had similar-sized testes at an age of 30–40 d suggesting that a minimal gonad size can be reached in just over a month. Nevertheless, as the cooler-season males continued to grow, the gonad continued to reach an appreciably greater size, for the same-sized individual. Thus, environmental constraints (such as temperature, food availability, or light levels) produced a different allometric gonad-soma relationship in this species which was not apparent in *L. chinensis*.

The fact that *I. pygmaeus* has a short lifespan and rapid growth may account for the lack of females with mature ova. It is possible that ovum maturation could take place very rapidly just before egg deposition. Therefore, it could be difficult to capture females with mature oocytes unless it was just prior to egg deposition. Alternatively, females with ripe ova may not have been near the water surface and therefore not available for sampling.

Idiosepius pygmaeus appears to be employing a 'trade-off' in its seasonal reproductive tactics, that is, benefiting from one process bought at the expense of another (Begon et al. 1986). During the cooler period of the year, growth is slowed (presumably as a result of metabolic responses to temperature), therefore lifespan is increased as a necessity, since individuals take longer to reach adult size. As a result, *I. pygmaeus* appears to change its tactics by partitioning a greater amount of energy into gonads over the longer lifespan. Although a longer time-period is taken to reach maturity, there would be a reproductive advantage in that possessing larger gonads would increase reproductive output. A similar situation has been shown to exist with teleost fishes. Stearns (1976) has provided evidence from several species of teleosts, showing that the ratio of ovary weight to body weight (as a measure of reproductive effort) increased with age.

The fact that this phenomenon occurs in *I. pygmaeus* and not the larger *L. chinensis* may be due to the need for *I. pygmaeus* to maximize its reproductive chances because of the greater nearshore habitat variability, or because of the greater constraints this species faces due to its small body size.

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